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THE CALCIUM CONTENT OF THE FOLIAGE OF SAL AND ITS COMMON ASSOCIATES IN THE DUN VALLEY*

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In the " Manual of Indian Silviculture " Champion (see Champion and Trevor 1938, p. XII) writes that " tropical forestry has, in fact, to build up its own silvicultural science, for experience has already taught that the differences from temperate forestry are often not merely differences in degree, but are liable to be differences in kind ". In the revised edition of this book (Champion and Griffith, 1947) while maintaining the view of the original author it has been emphasised that the study of ecology, tree physiology, and edaphic relations of plants is of fundamental importance in building up sound silviculture for India.

Our knowledge of these aspects of plant's growth for Indian forest trees is, indeed, very meagre. The position prior to 1938 was summed up by Champion (*loc. cit.*, p. 1) as under : " In several fields, notably soil science and tree physiology, data from the forests of India are sadly lacking, and foreign experience has had to be accepted for the present." In spite of the great need for this knowledge in silviculture little advance was made during the period 1938-1947 and except for two recent preliminary accounts of edaphic relationships for sal and teak (Griffith and Gupta, 1947 ; 1948) and works of the Irrigation Department (Taylor, Mahendru, Mehta and Hoon, 1935 ; Hoon, 1935 ; 1939) on soil profiles under conifer species in the Kulu and Kashmir Himalayas there are practically no data on the ecology, or biology of forest soils for any of the Indian forest types.

So far as we know, there is no complete work on physiology or autecology of a single Indian forest species though volumes have been written on their silviculture (Troup, 1921). These works, though monumental in their own way do not contain data even on such fundamental

* Contribution from the Ecology Section of Silviculture Branch.

subjects as mineral nutrition of plants, or the role of foliar minerals on the development of soils and vegetation.

The position regarding forest ecology is a little different ; there are a number of publications on plant sociology or floristic ecology, most of which however, do not give physiologico-ecological relationships of forest trees to their environment for the simple reason that data on tree physiology and soil science at that time were not available. Modern ecology recognises, in addition to climatology, soil science and plant physiology as its integral parts and it is no longer possible to draw a line between any one of these aspects of plant's relation with the environment ; considered in the light of this definition most of the ecological publications on Indian forests are incomplete (Puri, 1950, 1950a).

As a result of this paucity of fundamental knowledge in forest ecology, including its nutritional aspects, the progress in silvicultural research in this country was essentially slow and the critical study of European silvicultural systems was not, or could not be systematically taken up before adoption in this country, with the result that serious problems of natural regeneration, healthy growth, or normal development of some of our important forest species have arisen. These problems have now assumed serious magnitudes, threatening the forest economy of the country.

For the successful solution of these problems and building up of sound silviculture for India the urgent need for intensive and extensive studies in the domains of tree physiology and ecology of Indian species is much more obvious now than it was before. An attempt has been made in the present paper to present some data on mineral content of foliage of sal and its common associates in the Dun Valley so that in conjunction with data from other aspects of plant's relation with the complex of environmental factors this could be applied to silvicultural problems of forest regeneration and growth.

The importance of the present study may be apparent from the fact that tree vegetation exercises a profound influence on the development of surface layers of the soil and seedling growth. By virtue of their capacity to absorb minerals from lower layers of the soil and bringing them annually to surface layers in tree litter, trees create conditions for, or against, their own reproduction. The mineral content of foliage of trees in a region of uniform climate, therefore, is an index of soil fertility and this throws important light on questions of regeneration and succession of forest communities (Puri, 1948).

Of all the minerals present in foliage of trees in this region Ca is by far in greater amount and the " influence of the calcium outweighs that of all the other bases combined. This is owing in part to the relatively large amount of calcium present, as well as to the nature of the cation " (Chandler, 1939, p. 4).

The calcium content of tree foliage has a marked effect on (1) pH and base status of the surface layers of the soil, (2) the population of micro-organisms under tree stands, (3) the rate of decomposition of tree litter and availability of minerals and plant nutrients in the surface layers, and (4) physical characteristics of the soil. In short, it determines to a

great extent the type of humus that develops under a forest stand, and the type of forest that succeeds the present community (Puri, 1950). Determinations were, therefore, made at present only of ash and Cao content in fresh mature leaves of trees.

Specimens were collected in the months of October-November, 1948 from the reserved forests of Lachiwala, Kansrao, Thano and Asarori, however, five species were gathered from plantation in the New Forest during the months of September-October of the same year. Mature leaves were taken from middle-sized trees or shrubs, and one sample constituted leaves from 9-10 trees growing generally within a radius of 90-100 feet. In the plantations it was not possible to get leaves from many trees and one sample was drawn from only 2-3 trees in most cases.

Leaves were dried in sun and powdered in a grinding mill, sieved and ashed on bunsen burners after determinations of moisture content by keeping in an oven for 2 hours at temperature of 65°C. The ash was dissolved in N/4 Hcl and Cao was determined by the usual oxalate method given by Loomis and Shull (1937, pp. 329-330). Two replicates were taken and in one or two cases when difference between two determinations was more than 2 per cent a third replicate was also taken.

We take this opportunity to thank Dr. R. S. Gupta, Soil Chemist, for his kind help in these determinations. Ashes of five samples were kindly determined by Dr. D. Narayanmurti, of W.P. & C.W. Branch and duplicate determinations of ash in most cases were done by Mr. Shiv Lall, laboratory attendant under our supervision.

The average results for ash and Cao are presented in Table 1. As there was no relation of moisture content with any of the two constituents these are not given in this table. A complete list is, however, preserved in ledger files of the Silvicultural Branch and can be readily had for reference.

In the table species are arranged in order of increasing ash content. The order shown here may be representative only for the area studied and it is likely that if species are sampled from widely different areas any one species may take up position 3 or 4 places up or down from its position in the table.

The species studied enter into the composition of different types of forests extending from Assam in the east and Ganjam in the south to Punjab in the north-west and have a different frequency distribution due mainly to differences in soil conditions and climate. The ecological status, or even the exact systematic position, *viz.*, ecotype, genotype, etc., of sal in different parts of the country is not clearly known. According to Champion (1933) it may be climatic climax with one set of associates in one area and in others it may be postclimax or preclimax with the same or another set of species. It cannot be therefore, expected that *Shorea robusta*, or any of its associates will have exactly the same amounts of ash and Cao in their foliage in different conditions, as are found in the Dehra Dun Valley on alluvia. Extensive literature on European and American species seems to show that under different conditions of soil and climate the same species behaves differently with regard to its mineral requirements, however, studies are in progress to collect data on this

Table

Ash and Cao in leaves of *Shorea robusta* and its common associates in the Dehra Dun Valley.

Species	Leaves	
	Ash % on air dry material.	Cao % on air dry material.
1. Pinus longifolia	3.57	0.56
2. Shorea robusta	5.38	1.46
3. Litsæa chinensis	5.60	1.15
4. Acacia catechu	5.95	2.03
5. Carissa spinarum	6.12	1.33
6. Lagerstrœmia parviflora	6.24	1.58
7. Bassia latifolia	6.29	1.93
8. Woodfordia fruticosa	6.32	2.30
9. Flacourtia ramontchi	6.60	2.21
10. Bauhinia sp.	6.76	2.21
11. Zizyphus xylopyra	6.78	1.82
12. Machilus sp.	6.87	1.41
13. Miliusa velutina	6.97	1.61
14. Stephegyne parvifolia	7.00	2.27
15. Flemingia chappar	7.07	2.02
16. Eugenia operculata	7.27	3.20
17. Eugenia jambolana	7.30	2.35
18. Bauhenia vahlii	7.65	2.05
19. Litsæa polyantha	7.65	2.12
20. Terminalia chebula	7.79	2.75
21. Mallotus philippinensis	7.83	..
22. Bauhenia retusa	7.85	3.73
23. Anogeissus latifolia	7.88	3.22
24. Ehretia lævis	7.99	2.09
25. Clerodendron infortunatum	8.01	2.67
26. Elæodendron glaucum	8.05	3.66
27. Cassia fistula	8.08	3.08
28. Terminalia tomentosa	8.19	3.00
29. Fleuggea microcarpa	8.28	2.97
30. Hollarrhena antidysenterica	8.39	2.25
31. Ficus bengalensis	8.50	2.70
32. Sterculia villosa	8.65	2.81
33. Gardenia turgida	8.70	2.09
34. Bauhenia malabarica	8.83	3.52
35. Randia dumetorum	9.24	2.51
36. Ougeinia dalbergioides	9.47	3.57
37. Milletia auriculata	9.62	2.81
38. Semecarpus anacardium	9.67	3.36
39. Grewia vestita	10.03	3.28
40. Bombax malabaricum	10.50	2.61
41. Casearia tomentosa	10.53	3.17
42. Oroxylum indicum	10.72	3.19
43. Bridelia retusa	10.75	1.30
44. Alstonia scholaris	10.86	3.17
45. Helicteres isora	11.15	2.44
46. Terminalia belerica	11.54	4.41
47. Trewia nudiflora	11.60	3.05
48. Grewia oppositifolia	11.75	4.40
49. Buchanania latifolia	11.90	2.42

Table—*contd.*

Species	Leaves	
	Ash % on air dry material.	Cao % on air dry material.
50. Garuga pinnata	11.95	3.59
51. Loranthus longiflorus	11.95	2.82
52. Careya arborea	12.24	3.02
53. Murraya kœnigii	12.26	3.89
54. Colebrookea oppositifolia	12.27	3.31
55. Ventilago calyculata	12.45	5.63
56. Cordia myxa	12.55	4.93
57. Limonia acidissima	12.70	4.12
58. Stereospermum suaveolens	13.48	1.67
59. Nyctanthus arbor-tristis	14.04	3.63
60. Bauhenia purpurea	14.55	4.03
61. Ardisia humilis	15.10	4.22
62. Adhatoda vasica	15.20	5.07
63. Ficus glomerata	15.65	6.23
64. Holoptelea integrifolia	16.09	6.53
65. Kydia calycina	16.27	6.00
66. Ficus cunia	17.94	4.73
67. Ficus hispida	23.35	3.84

point for Indian species. The different mineral requirements of a species in different geographical regions may be due to its being composite species composed of various ecotypes. An attempt is being made to study *Shorea robusta* from the entire zone of its distribution to see this point as well.

From the table, it appears that ash and Cao in foliage of species studied show a good deal of difference and accounting for small variations that may be found in trees of the same species growing in different climates and soils the differences between species growing on the same type of soil and in uniform climate shown here are large enough to assume that they have not only different physiological demands on the soil minerals, especially lime, but their effects on the development of the humus layer and vegetation in the forest are also different. It may be pointed out that in some American forest species foliar Ca increases with season and at the time of leaf fall leaves have the maximum amount of calcium in them (Chandler, *loc. cit.*). Studies are in progress to see this in *Shorea robusta*.

It is seen from the table that foliar Cao in *Shorea robusta* is very low and it is higher only to *Pinus longifolia*, *Litsæa chinensis*, *Carissa spinarum*, *Machilus* sp. and *Bridelia retusa*.

The highest figures for Cao (above 6 per cent) are found in leaves of *Kydia calycina*, *Ficus glomerata* and *Holoptelea integrifolia*.

The species with low Ca are non-exacting and those which contain high percentage of foliar Cao are exacting on soil bases.

From the table it will be seen that species can be grouped together in a number of classes on foliar Cao and these groups occur in nature on different types of soil.

1. A low quality sal occurs in association with the chir pine, *Lagerstræmia parviflora, Machilus* sp., *Litsæa chinensis, Stereospermum suaveolens*, etc., on bouldery soils in the Siwaliks. The foliar Cao in these species is below 2 per cent.

2. *Grewia vestita, G. oppositifolia, Anogeissus latifolia, Careya arborea, Semecarpus anacardium, Kydia calycina, Ficus cunia*, etc. contain more than 4 per cent of foliar Cao and form miscellaneous jungles, without sal, on calcareous conglomerate outcrops on scarp slopes (Kansrao) or steep slopes by streams (Lachiwala).

3. *Anogeissus latifolia, Bauhenia retusa, Casearia tomentosa, Nyctanthes arbor-tristis, Cassia fistula, Elaeodendron glaucum, Eugenia operculata, Ougeinia dalbergioides*, etc. contain between 3-4 per cent of foliar Cao and form a miscellaneous forest with a low quality and low percentage of sal at Maidan hill in the Valley.

The data for foliar Cao seems to show that species with similar requirements for soil minerals tend to occur on one type of substratum. Further work on determining foliar Cao in species that have a wide range of soil and climate is in progress and it seems desirable that full discussion of these results be postponed to a later occasion.

This study, however, makes it abundantly clear that species occurring in this area have different demands on soil minerals, and seem to show differences in physiological requirements. They may, therefore, react differently to one and the same type of silvicultural operation. The different types of silvicultural operations essentially upset the normal physiological and ecological balance in a community favouring or stimulating seedling growth at the expense of other ground flora communities. Thus, the exact knowledge of physiological changes in a community is essential. A fuller examination of this question shall be dealt later on.

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STUDIES IN INDIAN ANTHOCEROTACEÆ

1. The Morphology of *Anthoceros crispulus* (Mont.) Douin*

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Introduction

The genus Anthoceros Linn., has since long been a favourite subject of morphological and taxonomical studies. It is now over two hundred years since studies in this genus were commenced but still hepaticologists do not seem to have come to an agreement on all points. The genus, as it stands today, embraces over two hundred species of world-wide distribution, particularly abundant in the tropics. These species are conveniently grouped into two sections, *viz.* :—

(1) those in which the colour of the mature spore is *dark brown* to *black* and

(2) those in which the colour of the mature spore is *yellow*. (*Vide* Stephani, Species Hepaticarum V, pp. 972-1007 & VI, pp. 425-29).

The above grouping was probably a guide to the possibility of elucidation of the nature and the degree of differences, that exist between these two proposed sections of Anthoceros. A number of workers since 1925, when the last volume of Stephani's Species Hepaticarum appeared, have contributed to this aspect which has become the most important problem of the genus. Yet the problem is not finally settled, although Müller (1940) (as cited by Proskauer 1948, p. 263) and Proskauer (1948) have gone, as far as, to suggest a separation of these two groups of Anthoceros into two separate genera. The author undertook a detailed morphological and taxonomic investigation of the Indian species of the genus with a view to study the same problem. This paper deals with the morphology of *Anthoceros crispulus* (Mont.) Douin, a black-spored species.

Historical

The earlier work on the genus Anthoceros was mainly of a taxonomic nature. It was however, Hofmeister (1862), who for the first time, studied the morphological details of the genus. He studied the development of the young sporophyte and distinguished the three layers in a capsule *i.e.*, the central columella, the wall layer and the sporogenous tissue in between these two. He had also studied the development of the spore and the elaters from the sporogenous tissue. Leitgeb (1876 and 1879) closely followed the earlier researches of Hofmeister and threw more light on the development of the capsule. We are indebted to Hofmeister and

* Proskauer (Ann. Bot. N. S. 1948, XII, 237) considers *A. crispulus* (Mont.) Douin a synonym of *A. punctatus* Linn.

Leitgeb for much of our present knowledge about the details of the early embryogeny. Leitgeb held (as cited by Goebel, Flora 1927) that the first division of the embryo in Anthoceros is vertical and that the sporogenous tissue is derived from the *inner amphithecium*. He further corroborated the earlier views of Hofmeister on the development and the morphology of the spores and the elaters.

In 1899, Davis (Bot. Gaz. **28**) published the details of the sporogenesis in *Anthoceros laevis* L. which till now form the basis of our knowledge of the behaviour of the nucleus and the chloroplast in the spore-mother-cells of the genus. It is unfortunate that enough work has not been done in this direction in any of the other genera of the Anthocerotaceæ.

Stephani, in the first quarter of this century, published his monumental work, Species Hepaticarum, but this work is mainly of a taxonomic value.

In 1907 Campbell (Ann. Bot. **21**) segregated Megaceros Campb. from Anthoceros and in 1916 Stephani separated some species of Anthoceros which show, in his opinion, true elaters and included these under a separate genus *Aspiromitus St.* Under the genus Anthoceros, Stephani described about 200 species grouped under two categories, *viz.* (1) *Sporæ pallidæ*, (2) *Sporæ fuscæ*. He classified each group according to the regional distribution of the species.

Bagchee (1924. Ann. Bot., p. 38) worked out the spermatogenesis in *A. laevis*.

Campbell has added materially to our knowledge of the Anthocerotaceæ. His studies on Dendroceros Gott. (Ann. Bot. 1898) and other members of the group (Ann. Bot. 1907 and 1908) have furnished us the details of the embryogeny of the various genera of the Anthocerotaceæ. His discovery of abnormal sporophytes of *Anthoceros fusiformis* Aust., showing remarkable growth, provided him material for much speculation regarding the relationships of the Anthocerotaceæ (Ann. Bot. 1924 and Flora 1925).

In 1928 Bartlett (Ann. Bot. 42) published a valuable account of a comparative study of the development of sporophytes in the Anthocerotaceæ with special reference to Anthoceros. Her study, obviously, was undertaken to elucidate the degree and nature of differences that exist between the dark- and the yellow-spored species of the genus and also their relationships with the other genera of the group. She concludes that there are two distinct groups of species, black-spored and yellow-spored, in Anthoceros and that the differences in the details of structure and development are significant to qualify such a distinction. She further discusses the relationships of these two groups with Megaceros, Dendroceros and Notothylas Sull. Among the yellow-spored species according to her, the more primitive or the more reduced sub-group, headed by *A. hallii* (Aust.), shows nearness to Megaceros or Notothylas and forms a natural link between these genera and the higher yellow-spored Anthoceros represented by *A. hawaiensis* sub-group, while the black-spored group is rather less specialized and shows affinity with

Megaceros and Dendroceros. In her opinion the question of the affinities of the various genera in the Anthocerotaceæ is rather complicated but, all the same, she concludes that Anthoceros, if it is an outgrowth of any other genus, has been derived from Megaceros rather than from such a form as Notothylas.

Gœbel (1927 and 1930) studied Anthoceros and Aspiromitus on the basis of Indo—malayan species and, apart from other details, he put forth revised interpretation of the morphology of the elaters in the two genera, Anthoceros and Aspiromitus. He stated that the sterile cells of Anthoceros are ontogenetically the same as the elaters of Aspiromitus. They differ only in the degree of breakage in the sterile cells which is more in Anthoceros than in Aspiromitus.

W. Rink in 1935 (Flora 30) made a very important contribution on the comparative morphology, physiology and genetics of *Anthoceros* and *Aspiromitus*. According to him, the two genera, apart from the differences in the nature of the elaters, as was pointed out by Stephani (loc. cit), show also differences in the nature of *andrœcial opening, the wall of the antheridium and the chromosome number*. According to him, the diploid chromosome number in Anthoceros is 12 and in Aspiromitus it is 10. He has also studied the genetical behaviour of a species of each in detail.

Recently Proskauer investigated some British species of Anthoceros and published two papers in this connection (Ann. Bot. XII, 47 ; XII, 48, 1948). He has approached the problem with a new angle. In his opinion the British yellow-spored species of Anthoceros are vegetative variants of *A. lævis* L. and all the dark-spored British species are but variants of two native black-spored species, *A. punctatus Linn.* and *A. husnoti St.* It is not unlikely that similar studies of other closely allied species may lead to similar results in other cases. His cytological studies, especially those pertaining to the chromosomal bearing on heterothallism, are valuable. He suggests the separation of yellow-spored section of the genus into a distinct genus, *Phæoceros.*

A perusal of the literature on the genus thus shows that certain of the important details, both in the taxonomy and the morphology of Anthoceros, have not yet been finally settled. It was for this purpose, as also with a view to place in the hands of the students of the Indian Universities a detailed systematic and morphological account of some of the species, that Dr. S. K. Pande, who had made a very valuable collection of the various genera of the Anthocerotaceæ from all over India, suggested a detailed comparative study of a dark-spored and a yellow-spored species of Anthoceros and also of some species of Aspiromitus.

A. crispulus occurs in the plains of the United Provinces in a strictly restricted locality, about 26 miles South-East of Lucknow. A preliminary paper on this plant was recently communicated by the author to the Botany Section of the Indian Science Congress, Allahabad, 1949.

Acknowledgments

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Occurrence

Anthoceros crispulus (Mont.) Douin was first described by Nees (Eur. Leb. IV, 340, 1838) as a variety of *A. punctatus Linn.* Later J. F. Montagne (in Webb et Berth., Hist. ins. can. Bot : 64, 1840) gave it the variety name of *crispulus*. The name in vogue *A. crispulus* was given by Douin (Rev. Bry., p. 25, 1905). It is rather restricted and sparse though widely distributed throughout the world. It has been reported by Stephani (Sp. Hep. V, 1912-191) from Gallia (Europe), by Macvicar (Handbook of British Hepatics, p. 449) from Great Britain and by Blomquist (Bryologist 39: 67) and by Evans (Bryologist 27: 52) from United States of America. In India, the species was first reported by Pande and Ahmad (Proc. Ind. Sci. Cong., 1944) from the neighbourhood of Lucknow, where it grows in a moist and shady locality on the bank of shallow lake, near village Hussainganj, Bachrawan, about 26 miles from Lucknow. It is found growing profusely in a very limited area of about 30 ft. × 10 ft., lying on the SE bank of the lake. The thalli grow between the tall grasses (chiefly *Androp ogon muricatus* Leh.) and are thus doubly shaded from the sun, and during the months of December, January and February the soil always remains moist. Apparently, this set of congenial environmental conditions are the cause of its survival in the hot plains of the United Provinces. Mixed with *Anthoceros crispulus* is occasionally found *Riccia crystallina Leh.* and *R. frostii Aust.*

About the middle of December, when the young thalli are first visible, they appear as minute green specks and by the middle of January small green sporophytes (·5cm to 1 cm long) are seen. Mature sporophytes are available from the middle of February to about the end of March.

The winter sets in the month of November and is over by February. The mean maximum and minimum temperature during this period is 75°F and 45°F respectively. The coldest period is generally the 1st week of January. Average winter rainfall is 2-4 inches, distributed in December and January. The plants thus have a small growing period as compared to England and Europe where they are available in fruiting stage from July-November. During winter the habitat at Bachrawan is rather moist and humid. The moisture is present around the plants throughout the greater part of the day. The author has closely observed and collected the plants for the past few years but has never found any change in their vegetative characters. It is, however, possible that under comparatively drier conditions of growth the dorsal lamellæ may become more pronounced in size and number as stated by Proskauer (1948).

The solitary occurrence of *A. crispulus* in the plains of U.P. is rather remarkable. It has neither been reported by Kashyap (20) nor found in the large collections of Anthoceros by Dr. Pande from the various parts of India now under investigation by the author. As pointed out by Pande and Ahmad (1944), *A. crispulus* may possibly be growing somewhere

in the Kumaon Himalayas and it may have been brought down by the canal or river or else, it may have been brought from its British home sticking to the packing material kept along with some preserved food taken by the picnic parties usually frequenting the lake side.

Material and Methods

The Material for this study was collected by the author several times during two successive winters at different periods of growth. Some living specimens were also brought to the laboratory where, when grown under natural conditions, they flourished well. Thalli, at different stages of growth and development of the sex organs and the sporophytes, were fixed in various fixatives. Most satisfactory results were obtained with Form-acetic-alcohol and Flemming's weak solution. The washing and dehydration was done as usual. Sections were cut 4-10μ thick and stained with various combinations of safranin, gentian violet and light green. To remove the undesirable effect of osmic acid, hydrogen-peroxide was used.

Description

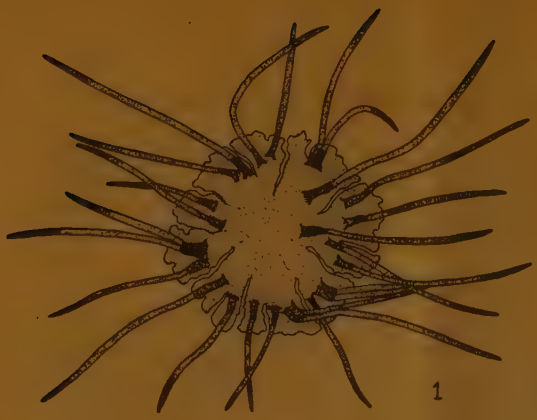
A. crispulus has been described by Macvicar (1926), Stephani (1916) and Schiffner (1937) and my observations are in agreement with those of the above authors. The thalli form bright-green or pale-green patches of variable size and may grow crowded together or scattered in between the grass stumps. They may form small rosettes '5-1'5 cms in diameter (Fig. 1) depressed in the centre and slightly raised towards the margins. The margin may be incised or lobed, the lobes being linear or cuneate. The dorsal surface is velvety or powdery in appearance due to the presence of many flat leaf-like lobed lamellæ (Fig. 29). The latter are one cell thick and several cells wide.

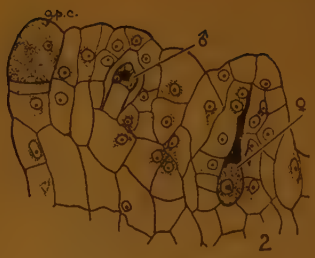
The thallus is spongy, and several cells thick in the middle. Mucilage is present in large lacunæ or cavities. *Nostoc colonies* are abundant and are spherical. These are visible to the naked eye as dense, opaque bluish green bodies. There is no midrib or structure akin to it. The bases of the sporophytes are seen in outer half of the thallus and are disposed in the form of a circle in the rosette. The ventral side is devoid of any lamellæ or tubers but bears numerous smooth rhizoids.

Structure of the thallus. In a T. S. the thallus shows prominent mucilage cavities. In the middle the thickness of the thallus is 30-40 cells and it gradually thins out towards the margins. *Nostoc* colonies are quite common. The growth of the thallus takes place by means of apical cells lying in the notches. Each apical cell cuts off segments as in other genera. The contents of the apical cell are densely stained (Figs. 2 & 12). The surface cells are 40-60μ × 30μ and are polygonal. Each cell has a single large chloroplast and a nucleus.

Sex organs

A. crispulus is monoecious and protandrous. The antheridia and archegonia occur on the same plant behind the apical cell and, in a well prepared section, these may be seen in various stages of development.





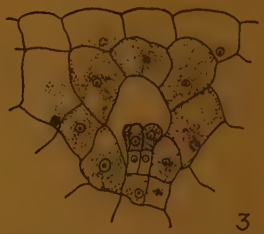


Fig. 1. A rosette showing circular disposition of sporogonia. × 2.
Fig. 2. L. S. of thallus showing apical cell (ap.c.), a young antheridial chamber (♂) and an archegonium (♀). × 370.
Fig. 3. A young antheridial chamber with young antheridia. × 540.
Fig. 4A. A young antheridium. × 370.
Fig. 4B. An older antheridium. × 370.
Fig. 5. T. S. of young antheridium. × 370.
Fig. 6. Antheridial chamber with 2 mature antheridia and 2 buds (×). × 540.
Fig. 7. An old antheridium showing wall cells in surface view. × 320.
Fig. 8. Young sperm mother cells. × 2050.
Fig. 9. Ripe spermatocytes. × 2050.
Fig. 10. Mature spermatozoids. × 2050.

Antheridium. Due to the presence of dorsal lamellæ the andrœcia are not visible to the naked eye. The antheridial chambers are scattered all over the thallus but are apparently more abundant in the neighbourhood of the sporophytes. They lie more or less deeply embedded in the thallus.

The antheridial initial arises as a dorsal segment of the apical cell. It divides by a transverse wall into an upper cell or the roof cell, and a lower cell or the antheridial initial. Soon a space develops between these two cells which gradually increases. The roof cell apparently divides by a periclinal wall parallel to the surface producing two cells lying one above the other. By subsequent vertical division these produce the two layered roof of the antheridial chamber (Fig. 6). Meanwhile, the antheridial initial, which lies at the base of the chamber, elongates and divides transversely into an upper cell which produces the body of the antheridium and a lower cell (Figs. 2 & 3) which forms the stalk. Later, presumably by two longitudinal walls, at right angles to each other, four antheridia are produced. This was not seen by the author. The number of antheridia in this species, as seen by the author, is upto 7. Some of these probably are due to budding from the bases of the primary ones (Fig. 6, ×) as reported for other species (Campbell, 1940).

As the antheridia grow, some of the adjoining cells of the thallus disintegrate and form mucilage which collects inside the chamber and the latter enlarges. As the development of the antheridium proceeds, periclinal walls separate a mass of central cells from the peripheral cells. The latter form a single layered wall (Figs. 4a, 4b, 5). Ultimately by a series of divisions the central cells produce the sperm-mother-cells. Each of these produces two small biciliate sperms (Figs. 8, 9 and 10). Details of spermatogenesis could not be followed.

The mature antheridium is a blunt club shaped body borne on a comparatively long stalk (Fig. 7). The latter is 4 cells thick and several cells long. The antheridial wall consists of numerous regularly arranged polygonal cells of variable size. On maturity of the antheridia, the roof of the chamber breaks down irregularly exposing the antheridia, which dehisce by an irregular rupture of the wall at the top. The actual dehiscence and liberation of sperms was not seen.

The spermatozoids lie as curved linear bodies in the spermatocytes. The cilia could not be demonstrated in the younger stage (Figs. 8 and 9). The body of the spermatozoid may be linear, curved with a little loop or in the form of straightened rod (Fig. 10). Proskauer (Ann. Bot., 1948) describes these, for *A. lævis L.* and *A. husnoti* St., as follows :—

" In *A. lævis* the sperms have a body 7-10μ long. The body shows some degree of residual curvature. Just behind the front end and beneath the flagella there is an elongated swelling, probably a blepharoplast. Cilia are long and 2 in number. The sperms of *A. husnoti* are exactly similar to those of *A. lævis* except that the (?) blepharoplast swelling is situated at the point of insertion of the flagella."

Archegonium : In younger stages the archegonia in *Anthoceros crispulus* are not easily recognisable, as they do not project much above the surface of the thallus. The neck consists of 6 tiers but these cannot

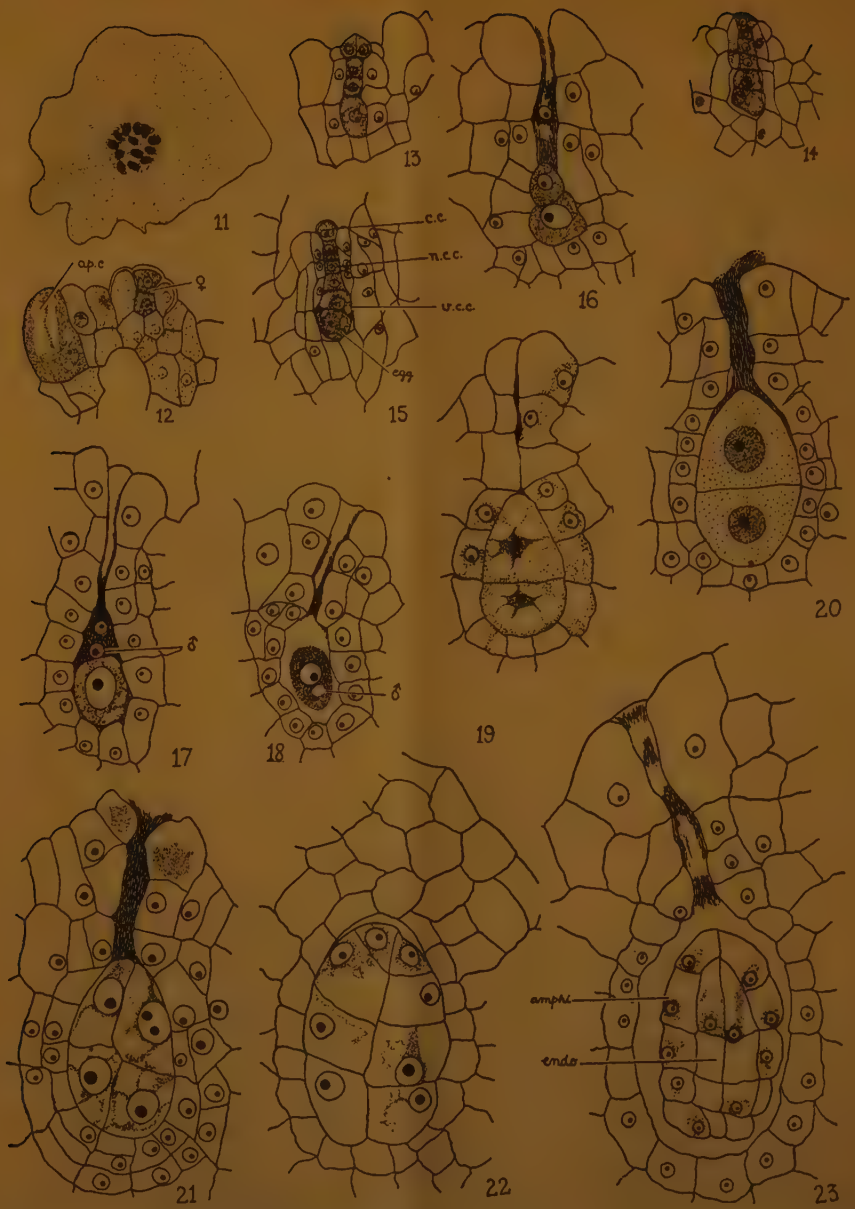


Fig. 11. A chloroplast with central pyrenoids. × 1700.
Fig. 12. L. S. of thallus showing an apical cell (ap.c.) and a two celled archegonium (♀). × 270.
Figs. 13 & 14. Young archegonia. × 270.
Fig. 15. Mature archegonium showing cap cells (c.c.), neck canal cells (n.c.c.), Ventral canal cell (v.c.c.) and egg. × 270.
Fig. 16. Archegonium showing disintegrating neck canal cells. × 540.
Fig. 17. Fertilised egg with male nuclei (♂). × 540.
Fig. 18. Fertilised egg with male nuclei (♂). × 540.
Fig. 19. Two celled Embryo. × 540.
Fig. 20. L. S. of 4 celled embryo showing only two cells. × 540.
Fig. 21. L. S. of 8 celled embryo showing only 4 cells. × 540.
Fig. 22. L. S. of 16 celled embryo. × 540.
Fig. 23. Embryo showing delimitation of endothecium (endo.) and amphithecium (amphi.). × 540.

be easily distinguished from the cells of the rest of the thallus. In Fig. 12 the archegonial initial can be distinguished a few cells behind the apex. The development of the archegonium is of the usual type as has been described by Campbell (1940). In a mature archegonium the neck-canal-cells are few in number (Fig. 15). The number of neck-canal-cells in Anthoceros as reported by various authors, is very variable. Janczewski (1872) states that there may be as many as twelve in *A. laevis*, but according to Campbell the number never exceeds 6 in Anthoceros, Notothylas, Megaceros or Dendroceros. According to the observations of the author, the number of neck-canal-cells in *A. crispulus* is usually 4.

The ventral canal cell in *A. crispulus*, as in other genera of the Anthocerotaceæ, is nearly equal in size to that of the egg (Figs. 14, 15 and 16). In a mature archegonium, the neck is comparatively narrow and the cap-cells are thrown off. The fertilized nucleus is larger than the normal egg nucleus (Fig. 17). After fertilization the oospore enlarges and almost fills the cavity of the venter (Fig. 17). A number of male nuclei (♂) were seen lying close to the oospore as well as in the archegonial canal (Figs. 17 and 18). A condition somewhat similar to this has been figured by Lotsy (1909, p. 79. Fig. 46) for Riccia.

Embryo

In *Anthoceros crispulus* the first division in the oospore is transverse to the long axis of the archegonium, producing two cells (Fig. 19). As far as the author is aware, in none of the other species of Anthoceros, so far worked out, such a condition has been reported. Hofmeister (1862) found an oblique septum in *A. lævis L.* According to Campbell (loc. çit 1940) the first division wall in *A. lævis* and *A. fusiformis* as well as *Notothylas orbicularis Sull.*, and *N. javanicus Campb.* (Campbell Ann. Bot. **22.** 1908) is longitudinal. Cases of longitudinal septum are known in Megaceros (Campbell Ann. Bot. **21,** 1907) Dendroceros (Campbell Jour. Linn. Soc. Lond. XXXVIII) and Notothylas (Campbell Ann. Bot. **22,** 1908). In a few cases, in *A. crispulus* oblique septa were seen but these were due to oblique sectioning of the embryo. According to Pande (1932) the first division wall in the fertilised egg of *N. indica* Kash. is transverse. In *N. orbicularis*, Mottier (1894) also reports that the embryo divides first by a transverse wall.

The second wall is at right angles to the first and is vertical (Fig. 20). This is followed by another longitudinal wall at right angles to the two preceding ones, resulting in an 8-celled embryo (Fig. 21). Thereafter the progress of the division is the same as described for other species of the genus (Campbell 1940). However, the upper and the lower halves of the 8-celled embryo divide by transverse walls before any periclinal septa are laid down in the uppermost quartet (*i.e.* before the beginning of delimitation of the amphithecium and the endothecium) (Fig. 22).

The first evidence of delimitation of amphithecium and endothecium was not seen by the author but by an observation of subsequent stages in the embryogeny, there is hardly any doubt that, as in the rest of the Anthocerotaceæ, it is initiated by the formation of periclinal walls in

Fig. 24. Differentiation of archesporium and structure of young foot (ft.). One of the amphithecial cells (×) is seen dividing. × 540.

Fig. 25. Older capsule showing a developing foot and the wall, archesporium (archi.) and endothecium (endo.). × 250.

Fig. 26. Foot showing columnar lining cells (c.l.c.) and central vacuolated cells (c.v.c.). × 320.

Fig. 27. Large foot as seen in an advanced sporophyte. × 250.

the uppermost tier of the embryo (Fig. 23). This septation extends to the next tier and when complete, separates the inner and the central cells, the endothecium, from an outer single layer of cells, the amphithecium. All this takes place while the capsule is quite young.

Foot:—The lowest two tiers arising from the lower half of the embryo, go to form the foot. The cells of these foot-forming tiers divide once longitudinally. The divisions in the lower layer occur quicker than in the upper layer resulting into a curvature in the lower layer (Fig. 24). The divisions in this external layer continue in longitudinal direction, thus increasing the curvature and the cells are columnar with denser contents. The divisions in the inner tier of the foot are rather irregular and a large number of thin walled vacuolated polygonal cells (c.v.c.) are formed to, fill up the space between the external columnar layer and the seta (Figs. 26 and 27). A fully developed foot is deeply rooted, anchor-shaped structure clearly delimited from the gametophytic tissue (Fig. 29). The cells of the thallus adjacent to the foot cells get flattened as if due to pressure exerted by the growing foot (Figs. 26 and 27). The foot and the gametophytic tissue get separated and a space appears between them even when the foot is young (Fig. 24). This space is filled with mucilage and small flattened cells.

Archesporium :—As in other species of Anthoceros, periclinal walls are laid down in the cells of the *amphithecium* which delimit an inner archesporial layer of cells with denser contents and large nuclei next the endothecium. In Fig. 24 are seen cells of the amphithecium one of which has just divided and the next below it has a spindle (×) lying across the axis. Some of the amphithecial cells are yet undivided. Thus it is apparent that the sporgenous tissue in *A. crispulus*, as in *A. lævis*. and *A. fusiformis*, originates from the amphithecium.

The archesporium caps the endothecium. Cell divisions in the endothecium result into a 16 cells thick column, as seen in a transverse section. Divisions in the outer layer of amphithecium result into a 4-5 cells thick sterile wall (Figs. 28 and 30). On the exterior this wall is limited by an epidermis (Fig. 30), the cells of which have thickened radial and tangential walls. When all the layers of the sporophyte are well established the meristematic activity gets confined to the region of the seta lying just above the foot (Fig. 29). Various tissues of the capsule are later produced from the cells of the seta.

Involucre :—During the early period of growth of the young embryo a covering or sheath of gametophytic tissue appears over the embryo. This sheath or involucre, grows, keeping pace with the growth of the embryo for some time (Fig. 29 invol), but at last the sporophyte overgrows the involucre and breaks through it leaving a frilled constricted mouth. Henceforth the involucre grows very little. Internal structure of the involucre is like that of the thallus. The cavities in the involucre are filled with mucilage. It is because of the presence of this mucilage that dehydration and infiltration in young embryo is rendered more difficult. The difficulty can, however, be overcome to some extent, by incising the tissue of the involucre with a sharp scalpel. The length of the involucre is a fairly constant feature and averages about 2.5-3 cm.

Sporophyte

The young sporogonia are bright green in colour and project upwards like horns or bristles. They are fairly numerous on a rosette and are usually cylindrical and straight, but the outer capsules may sometimes be slightly curved. In mature sporogonia the tips are blackened as the spores mature and the blackening progresses downwards from the tip. A t.s. through an undehisced sporogonium (Fig. 30) shows acentral 16 celled columella, followed by a wide cavity, full of spores and pseudœlaters. Outside the spore cavity, is the wall, bounded by the epidermis. The wall cells are nucleated and each contain a single chloroplast.

The epidermis shows 2-4 shallow grooves, which mark the future lines of dehiscence (Fig. 30 d.l.) of the capsule. But the capsule dehisces along two sutures only. In Anthocerotaiceal a case of 4-valved dehiscence of the capsule is reported in *N. indica* by Pande (1932).

The capsule wall shows distinct and well developed functional stomata irregularly distributed on its surface. The guard cells are large and uninucleate. The stomata measure 56 × 36μ.

Sporogenous layer :—The process of sporogenesis could not be studied in detail due to abundant mucilage in the spore cavity, which interferes with the proper dehydration and infiltration. The sporogenous layer is uniformly one cell thick all over. In younger stages all the sporogenous cells are rectangular and slightly broader than long. These have denser contents and are marked by a greater affinity for the stains. As the cells of the sporogenous layer mature, a difference in their shape is usually seen and soon an alternation of spherical large spore-mother-cells (sp. m.) with elliptic pseudœlater-mother-cells (el. m.) is noticeable (Figs. 32A and 32B). The young spore-mother-cells are round or elliptic, with a small nucleus which does not stain very strongly. These continue to enlarge and after some time the chloroplast appears which is soon divided into two by ordinary process of halving (Fig. 34). The development of the spore could not be studied. The spore tetrads, when young, are large and spherical with the spores developing inside these.

The pseudœlater-producing-cells, which alternate with the spore-producing cells, soon show transverse or oblique divisions. The pseudœlater-mother-cells divide a number of times to produce a loose net of sterile cells which on dehiscence breaks up into 1-3 celled individual pseudo-elaters. Owing to the small size of the nucleus, nuclear divisions could not be followed.

Spores :—The spores are black to dark brown. Young and immature spores are lighter in colour. They are hispid (Fig. 35) with rather short pointed spines of *A. punctatus L. type.* The triradiate mark is visible. They measure about 45-50 μ.

Pseudœlaters :—The pseudœlaters are usually 1-2 celled, sometimes 3 celled, thin hyaline, smooth walled, frequently branched structures. They are 100 μ long and 10-15 μ broad (Fig. 36).

Dehiscence :—The splitting of the capsule into two valves is evidently the normal phenomenon soon after the capsule is mature. In *A. crispulus*,

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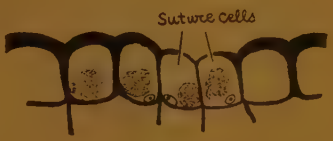

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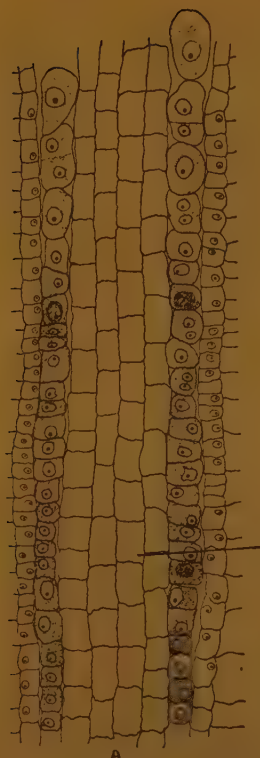
Fig. 28. A young sporophyte showing the wall of the capsule, complete sporogenous layer (archi.), columella (col.) and the foot (ft.). × 250.

Fig. 29. L. S. of the thalus showing lamellæ (lam.) and a young sporophyte (cap) yet enclosed in the involucre (invol.) × 37.

Fig. 30. T. S. of a sporophyte showing 2 functional dehiscence lines (d.l.). × 250.

Fig. 31. A portion of the epidermis through suture cells. × 750.



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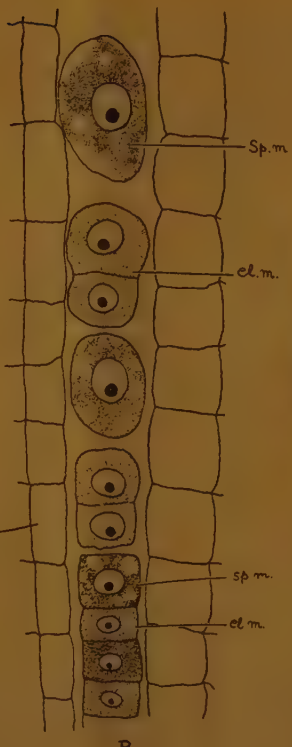

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Fig. 32A. Sporogenous tissue and columella (col.). × 370.
Fig. 32B. A portion of sporogenous tissue showing elater-mother-cells (el.m.) and spore-mother-cells (sp.m.). × 750.
Fig. 33. Later stage in the differentiation of the spores and elaters (el). × 750.
Fig. 34. A young spore-mother-cell with chloroplast dividing into two. × 750.
Fig. 35. Spore. × 500.
Fig. 36. Pseudoelaters. × 370.

dehiscence of the capsules in Lucknow starts by the end of February when the weather is dry and cool due to the advent of the spring. The sporophytes, as they mature, become brownish turning ultimately black. Ripening of the capsules proceeds from the tip downwards.

Soon the blackened sporogonia begin to show small split near the tip which, as the capsule dries up, gradually progresses downwards. The split is along two opposite external grooves present on the dorsal surface of the capsule which represent the lines of dehiscence. The lines of dehiscence usually meet at the tip and in such cases the split of the valves is complete and the valves do not remain attached at the tip. In equally numerous cases the split valves were seen cohering at the tip. In a few cases it was observed that the conical tip of the capsule was present only on one of the valves, the lines of dehiscence having joined slightly below the tip on one side. All these different cases suggest that the lines of dehiscence

either (*i*) fail to meet at the tip (Fig. 39)

or (*ii*) meet at the tip in the normal way (Fig. 40)

or (*iii*) meet on one side below the tip (Fig. 41).

Each of the valves when dry becomes strap shaped and twisted, liberating its mass of spores and pseudœlaters. The twist is, however, not very strong and the valves are mostly flat. The valves show hygroscopic movements which are more pronounced when drying is quick, *e.g.* under a drop of alcohol. The spores and pseudœlaters are expelled with very little force. On wetting, the sides of the flattened valves converge and the valves come together almost occupying the same position as in an undehisced capsule (Figs. 37B, 38B, 42 and 43).

Discussion

In the latest publication by Proskauer on the morphology of Anthoceros (loc. cit) a number of interesting facts have come to light. The finding, which has a direct bearing on this paper is that *A. punctatus L.* under drier conditions of growth gives rise to smaller plants with shorter sporophytes and with a rugged or crisped appearance of the thallus very much like *A. crispulus*. He however contends that this velvety or rugged appearance is due to various causes and gives 8 different conditions which contribute to this appearance among which only one is the development of the dorsal lamellæ. Even MacVicar (1926) observed that in *A. crispulus* sometimes the thallus is less divided and lamellæ are less numerous and in such cases it is difficult to find a limit between *A. crispulus* and *A. punctatus*. In India this species grows on damp soil on the bank of a lake shaded by tall grasses under a tropical winter sun. The humidity is maintained, to some extent, by surface precipitation. The thalli are rather small 0.8 mm-1.5 cms in diameter, spongy and with comparatively longer sporogonia than reported by MacVicar (loc. cit) and Proskauer (loc. cit). Smaller sporogonia, 15 mm long, are also abundant whereas the usual size, in mature plants, is about 20-25 mm long. The species is under observation since the last 6 years. The thalli in nature look like specks of green velvet. The thallus is not much divided as reported by MacVicar and Proskauer for the British specimens and the rugged or

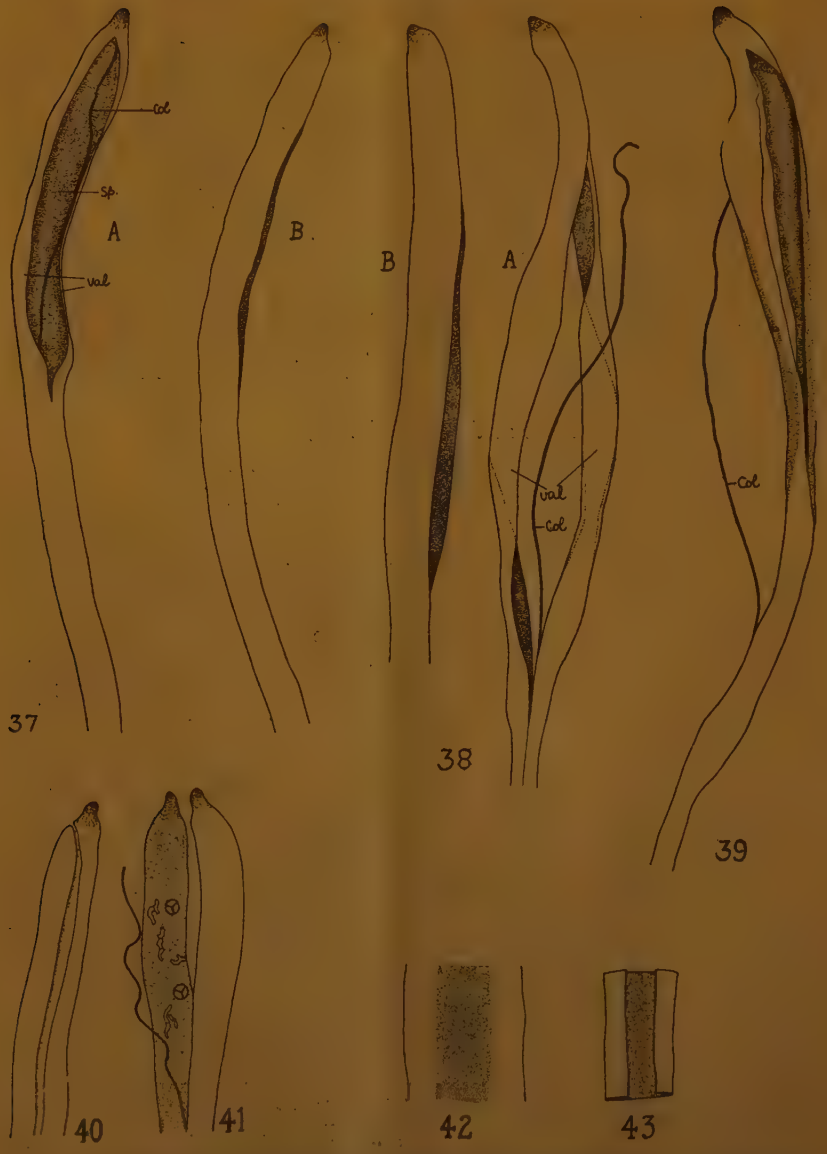

Fig. 37A. Single suture dehiscence in a capsule showing columella (col.) spore mass (sp.) and valves (val.). × 40.
Fig. 37B. The same on wetting. × 40.
Fig. 38A. Bivalved dehiscence showing the twisting of valves. × 40.
Fig. 38B. The same on wetting. × 40.
Fig. 39. A capsule tip where dehiscence lines fail to meet at the tip. × 40.
Fig. 40. A capsule tip with dehiscence lines meeting laterally. × 40.
Fig. 41. A capsule tip with dehiscence lines meeting medianly. × 40.
Fig. 42. A piece of valve in dry condition. × 140.
Fig. 43. The same piece of valve in wet condition. × 140.

crisped appearance is due to lamellæ only. In a t.s. (Fig. 29 lam) the lamellæ are seen as fairly well developed thin outgrowths on the dorsal surface. The details of structure conform to *A. crispulus*. The species has maintained its vegetative character since it was first observed.

The number of Antheridia in *A. crispulus* is remarkably large as compared to the usual number of antheridia in the black spored species of Anthoceros. Bartlett gives the normal number as 4 or more. It may be pointed out that the antheridia in this species are also comparatively larger and club shaped. In other species these are generally spherical.

A rather unusual feature of *A. crispulus* is the occurrence of a transverse septum as the first wall of division in the oospore. In this respect the species differs from all the other species of Anthoceros, so far investigated. According to Campbell (1907 and 1908) in *Megaceros tjibodensis* Campb., and *Notothylas javanicus* Campb., and *N. orbicularis* Sull., the first division wall in the fertilised oospore is longitudinal although only oblique septa have been figured. A longitudinal septum is also reported for *Notothylas breutelli* by Lang (1924) and *N. levieri* by Pande (1934). In *N. indica* kashyap, Pande (1932) found that first division wall in the fertilised egg is transverse and a similar condition has been given for *N. orbicularis* by Mottier (1894). Thus the evidence, so far available shows that both the conditions of transverse as well as longitudinal division of the oospore are present in the various genera of the Anthocerotaceæ.

Summary

1. The thallus of *A. crispulus* is spongy due to the presence of large mucilage cavities and shows strap shaped lamellæ on the dorsal surface.
2. The species is monœcious. Androœcia are inconspicuous because of overlying lamellæ. Each chamber contains 6-7 antheridia. Development of the antheridium is of the normal type. Mature, antheridium is a club shaped, medium sized, stalked body. The antheridial wall consists of polygonal cells.
3. The archegonium develops on the dorsal side. Each archegonium has a large venter. The egg and the ventral-canal-cell are of almost equal size, and the neck has 4 neck-canal-cells. The cap cells are prominent.
4. During fertilization a number of spermatozoids enter the archegonial neck, but only one of these fuses with the egg.
5. The first division of the oospore is transverse. This is followed by two longitudinal walls at right angles to each other. Thereafter two more transverse walls are laid down, one in each of the two halves of the embryo, before the separation of tne amphithecium from the endothecium is effected.
6. The lower half of the embryo goes to form the foot. The latter is clearly delimited from the thallus and is deeply anchored in it, but is not haustorial.
7. The involucre is spongy and its size, irrespective of the length of the sporophyte, is fairly constant.

8. The sporogenous layer arises from the amphithecium and is uniformly one cell thick. The spore-and the elater-mother-cells alternate regularly with each other.
9. The columella is always 16 cells thick, as seen in a transverse section, and is smooth.
10. The spores are large, hispid and black. The pseudœlaters are 2-3 celled. They are thin walled and are sometimes branched.

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CONTRIBUTIONS TO THE EMBRYOLOGY OF STERCULIACEÆ—II

Waltheria indica Linn.

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The present paper deals with the development of the ovule, embryo sac and embryo in *Waltheria indica* L. The organogeny of the flower and microsporogenesis in this species have already been described in the first of this series of contributions (Rao, 1949*a*). The material for the present investigation was collected from the Andhra University grounds where the plant grows as a weed. Formalin-acetic-alcohol was used as the fixative with satisfactory results. The material was dehydrated and

embedded in paraffin according to the customary methods. Sections were cut 4-8 μ in thickness and stained with Heidenhain's Iron-alum hæmatoxylin or with a combination of Safranin and Fast Green.

The flowers of *Waltheria* occur in densely crowded axillary and terminal clusters. They are bracteate and shortly pedicillate ; the perianth is 5-merous and slightly gamophyllous. There are five antipetalous stamens, slightly connate at the base. The gynœcium differs from that of the other members of the family in being unilocular and showing only two superposed ovules, of which only one develops in the fruit (Fig. 5). The style is solid and excentric and shows an irregularly lobed stigma (Fig. 4).

The ovules are top-shaped, anatropous and bitegmic, with their micropyles facing the base of the ovary. Though both the integuments arise simultaneously on the ovule primordium, the outer grows faster than the inner as in other members of the family (Fig. 2). Ultimately both the integuments close up to form a zig-zag micropyle (Fig. 3). At first both the integuments are two cells thick. In the mature ovule, the outer remains so all over except in the micropylar region, where it becomes 3-4 cells thick, while the inner integument becomes 6-7 cells in thickness throughout its length (Fig. 37). The epidermal layers are composed of cubical and regularly arranged cells, while the cells of the remaining layers are irregularly disposed. Early in the development of the ovule the cells of the outer layer of the outer integument lose their protoplasmic contents and get filled with deep staining contents, probably mucilage. The cells of the sub-epidermal layer of the inner integument, which are much larger than those of the other layers, also get filled with similar contents. One interesting feature in this process is that the cells in a cap-like zone around the micropyle do not accumulate such contents, but remain normal and living till the pollen tube has penetrated the embryo sac. Only after fertilisation they change like the rest. The same feature has been observed also in the ovules of *Melochia corchorifolia* (Rao, 1949*b*). This possibly prevents the injurious effect of the chemicals on the delicate pollen tube (Fig. 3). The outer integument adheres loosely to the inner so that an air space is often seen between the two in microtomed sections of mature ovules. The ovule develops a blunt hump-like outgrowth on the chalazal end as in *Dombeya* and *Melochia*. A fertilisable ovule measures about 700 μ in length, of which the hump-like outgrowth measures 150 μ. The cells in the chalazal region stain deeply due to the presence of tannin in them ; a similar dark-staining zone was found in the ovules of the other members of the family like *Melochia*, *Pterospermum* (Rao, 1949*a*, *b*), and *Theobroma* (Cheesman, 1927), and also in *Corchorus olitorius* (Banerji, 1932) and *Bombax* (observed by the writer), so that this feature seems to be a characteristic for the whole order Malvales.

The nucellus is massive. It is composed of relatively large and more or less regularly arranged cells. An epidermal cap 2-3 cells in thickness is present. In the mature ovule all the 3-4 layers of cells formed by the primary parietal cell get crushed by the growing embryo sac and only the cells of the epidermal cap persist above the micropylar region of the embryo sac. About seven layers of cells are present at the sides of the embryo sac about its middle. When the embryo sac is in 2- or 4-nucleate

Figs. 1-5. *Waltheria indica* L. Various stages in the development of the ovule and the seed. Fig. 1, × 198 ; Fig. 2, × 180 ; Fig. 3, × 75 ; Fig. 4, × 45 ; Fig. 5, × 30.

stage, one or two layers of nucellus cells immediately below its antipodal end become thick walled and lose their cell contents. In course of time, the cells between this layer and the vascular strand also become thick walled. As these cells are more or less in regular rows, they appear as a *hypostase*-like strand (Fig. 15) and possibly facilitate the conduction of food materials from the vascular strand into the embryo sac.

Megasporogenesis and Embryo sac

The two ovules arise as papillate outgrowths at the base of the ovary. As further growth of the ovary is not uniform at its base, one side of the ovary grows up faster and carries with it the funicle of one ovule ; consequently the style also becomes excentric (Fig. 4). The primary archesporium in the ovule differentiates even before the ovary wall has closed up to form the style (Fig. 1), when the ovule primordium shows

only a slight curvature at its tip. The integument initials appear a little later. As in other genera of the family, the archesporium is multicellular to start with, consisting of hypodermal and sub-hypodermal cells (Fig. 6). Out of these, as a rule, only one axially placed hypodermal cell functions further, while the rest merge into the nucellus. Two functional archesporial cells were seen only in the very early stages of development of the ovule (Fig. 7). After a slight enlargement, the functional cell cuts off the primary parietal cell to the outside and the megaspore mother cell to the inside. The parietal cell divides first periclinally and then cell divisions occur in all planes resulting in a parietal tissue of three to four cell layers all of which, as already described, get crushed by the enlarging embryo sac.

The megaspore mother cell remains in the resting stage for a fairly long time prior to the two meiotic divisions. It slowly enlarges in size ; during this period about four layers of parietal cells are formed over it and the outer integument reaches the level of the nucellus apex (Fig. 8). The megaspore mother cell has an elongated and tapering form as in other genera of the family. The two meiotic divisions occur in a normal manner and result in a linear tetrad of megaspores which are almost similar in appearance. Usually the lowest megaspore enlarges and functions further (Fig. 9), though in one case the third megaspore from the micropylar side was seen to enlarge and crush the chalazal most megaspore (Fig. 10). The shape of the functional megaspore unlike that of the other genera studied, is almost spherical, the nucleus being evenly surrounded by the cytoplasm. Gradually, however, two terminal vacuoles appear and the polarity becomes evident. By three free nuclear divisions of the nucleus of the functional megaspore the 8-nucleate embryo sac is organised (Figs. 11-13).

The egg apparatus shows the normal structure already described in *Pterospermum* (Rao, 1949*a*). The synergids which are as large as the egg show two unequal terminal vacuoles and hook-like protuberances on their sides. No filiform apparatus was noticed. The egg is flask-shaped, with a large vacuole towards the micropylar side and a nucleus situated in scanty cytoplasm at its chalazal end. The two polar nuclei lie free but closely pressed together near the egg. The antipodals are not ephemeral but persist (though in a degenerate condition), till the pollen tube has penetrated the embryo sac (Fig. 17). The cytoplasm of the sac is mostly aggregated around the polar nuclei, a little extending in the shape of fine strands to the antipodal end. It shows some starch grains (Fig. 16). A young embryo sac measures about 100 μ in length and 45 μ in diameter. After it is organised it shows rapid and considerable growth and in the fertilisable ovule measures about 300 μ in length and 70 μ in diameter (Figs. 13 and 14). As the thick walled cells in the nucellus stand below the antipodal end of the sac and do not cover up its sides, the embryo sac expands uniformly all over and becomes cylindrical or slightly barrel-shaped and does not show the tubular antipodal end characteristic of the embryo sacs of *Melochia* or *Pterospermum* (Rao, 1949*a*).

Fertilisation

Pollen grains are caught by the glandular protuberances of the stigma where they germinate. The pollen tube bores its way through the solid

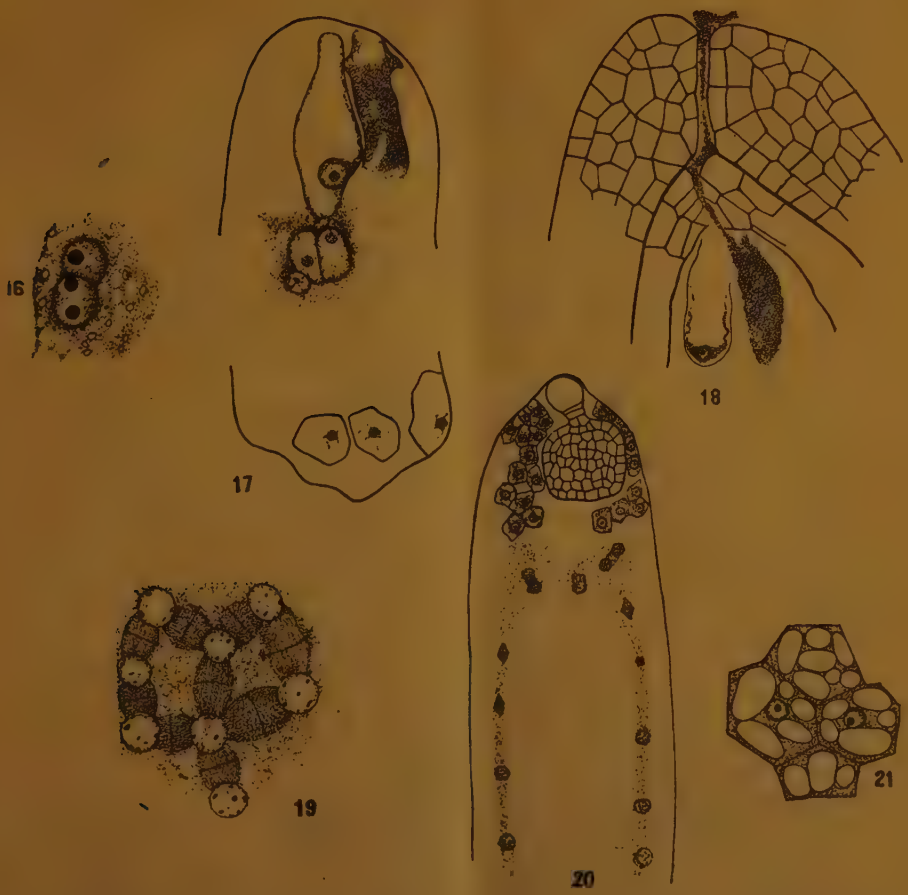
Figs. 6-15. *Waltheria indica* L. Fig. 6, ovule primordium showing multicellular archesporium. Fig. 7, two functional archesporial cells which cut off primary parietal cells. Fig. 8, megaspore mother cell just before meiotic divisions. Fig. 9, linear tetrad of megaspores with the lowest functional megaspore enlarging. Fig. 10, linear tetrad with the third megaspore functioning. Figs. 11 and 12, 2–and 4–nucleate stages of the embryo sac. Figs. 13 and 14, young and mature 8–nucleate embryo sacs. Fig. 15, chalazal region of the ovule showing the hypostase-like strand. Fig.

tissue of the style and traverses along the inner margin of the ovary wall. Taking a bend near the base of the funicle it enters the micropyle. Hence fertilisation is porogamous. Penetrating the epidermal cap, the pollen tube enters a synergid through its micropylar end and empties its contents therein. As a result the synergid gets filled with dark staining contents, while the unaffected synergid persists a little longer, practically unaltered (Fig. 18). The affected synergid bursts at its base and discharges the two male nuclei into the embryo sac ; the tube nucleus seems to degenerate early and was never found in any of the embryo sacs at this stage (Fig. 17). One male nucleus fuses first with one of the polar nuclei (Fig. 16) and later a triple fusion nucleus is formed, as was also observed in *Melochia* (Rao, 1949*b*), and *Corchorus* (Banerji, 1932). The fertilisation of the egg follows a little later and by the time it is complete, a few endosperm nuclei are already formed (Fig. 23). The two gametic nuclei at the time of fusion are in the early prophase (Fig. 22).

Up to the fertilisable embryo sac stage, both the ovules in an ovary develop normally. As the upper ovule stands nearer to the style it has greater chances to be fertilised earlier than the lower one. Hence usually the upper ovule persists and forms the seed. Degeneration of the lower ovule commences soon after the upper gets fertilised ; it gets completely shrunken even before the fertilised egg in the upper ovule has divided (Fig. 5). The cause for its degeneration seems to be physiological and not mechanical pressure exerted by the growth of the upper ovule because by this time the upper ovule does not show any appreciable growth. After fertilisation, the food materials seem to be diverted into the fertilised ovule so that the lower ovule gets starved out. This is also borne out by the fact that the richly protoplasmic nucellus cells degenerate first, while the cells of the integuments persist intact for a longer time (Fig. 5).

Endosperm

The first division of the primary endosperm nucleus occurs almost immediately after triple fusion. Further divisions are at first free nuclear, the resulting nuclei being commonly multinucleolate. Divisions in the endosperm nuclei do not occur simultaneously, but proceed in waves starting from the micropylar region of the embryo sac. As the divisions occur in regular sequence, sometimes all stages from telophase to the metabolic nuclei can be encountered in passing from the micropylar to the antipodal regions of the embryo sac (Fig. 20), as was reported in *Allmania nodiflora* and *Amarantus viridis* by Kajale (1940). There is at first a greater aggregation of the endosperm nuclei in the micropylar region of the embryo sac around the embryo (Figs. 20 and 23). The endosperm becomes cellular just before the cotyledon primordia are organised in the embryo, the cell wall formation commencing at the micropylar end (Fig. 19). In Fig. 20 is shown the micropylar part of the embryo sac in which the endosperm around the embryo has already become cellular, while free nuclear divisions are still continuing towards the chalazal side. Up to this stage the endosperm remains thin, but henceforth it enlarges rapidly encroaching upon the nucellus. A similar condition was observed in *Melochia* (Rao, 1949*b*) and *Theobroma Cacao* (Cheesman, 1927). Ultimately the whole of the endosperm gets cut up



Figs. 16-21. *Waltheria indica* L. Fig. 16, fusion of one male nucleus with a polar nucleus. Fig. 17 upper and lower parts of an embryo sac at the time of fertilisation. Fig. 18, pollen tube penetrating a synergid. Fig. 19, cell wall formation in the endosperm. Fig. 20, micropylar part of an embryo sac with a globular embryo and divisions in endosperm nuclei. Fig. 21, endosperm cells packed with starch grains. Fig. 17, × 473 ; Figs. 18 and 19, × 675 ; Fig. 20, × 150 ; Fig. 21, × 370.

into uninucleate cells which become densely packed with starch grains (Fig. 21).

Embryo

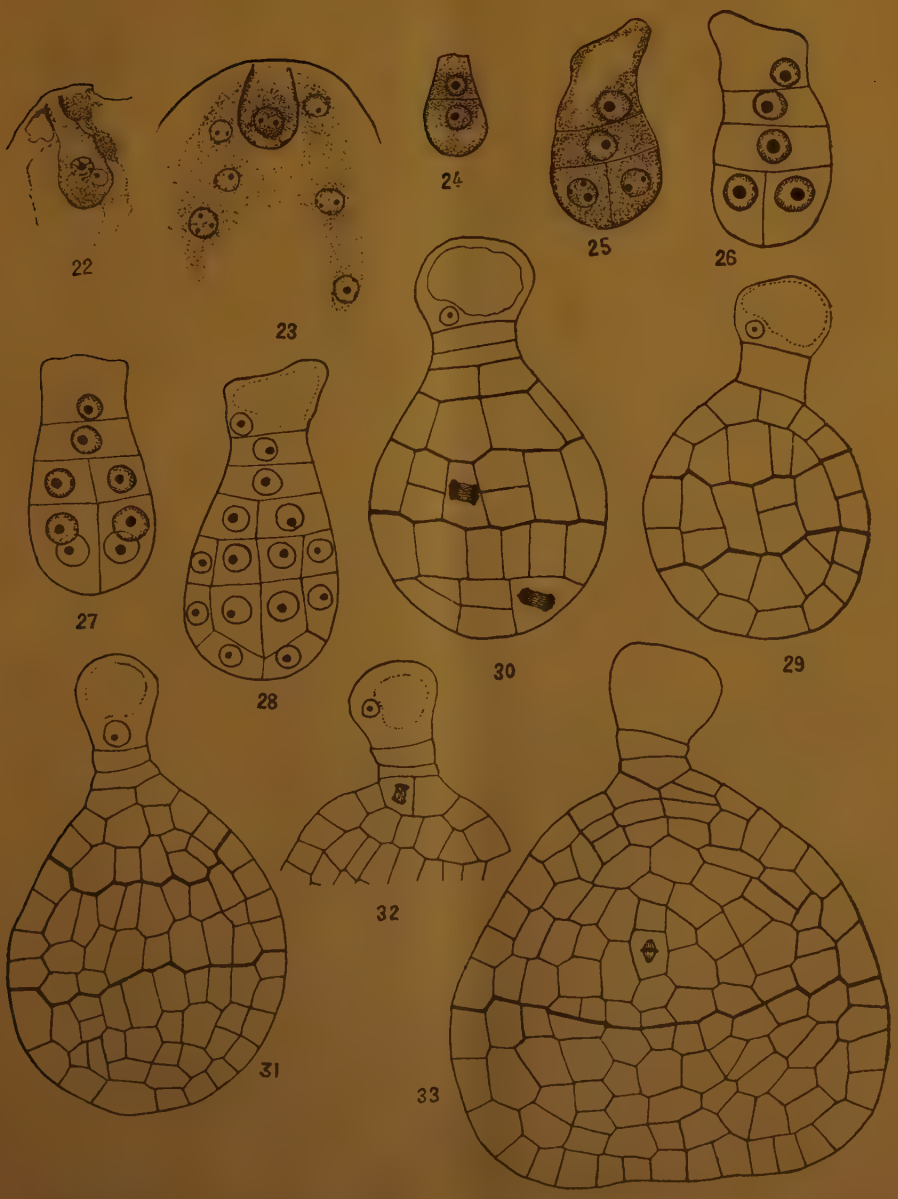
Development of the embryo corresponds in general to the *Asterad*-type of Johanson (1945). The presence of a suspensor and the absence of the epiphyseal cell in the terminal tier shows that it keys out to the

Polygonum-variation of this type. The first division of the fertilised egg is transverse resulting in the basal and terminal cells (Fig. 24). The next division in both the cells occurs simultaneously, division in the terminal cell being longitudinal while that in the basal cell is transverse (Fig. 25). Thus by the time the first longitudinal division occurs, the proembryo is three cells long. The derivatives of the terminal cell divide once more in a longitudinal manner in a plane at right angles to the plane of the first division, resulting in quadrants (Fig. 26). Meanwhile the lowest cell divides in a transverse manner so that the young embryo becomes four cells long (Fig. 26). The three terminal cells take part in the formation of the embryo and the basal cell forms the suspensor. The derivatives of the terminal cell give rise to the stem tip and cotyledons ; the second cell forms the hypocotyl region and the third cell forms the root tip except its dermatogen and root cap which are filled out by the hypophysis cell formed from the basal suspensor cell. Thus both the terminal and basal cells formed after the first division of the fertilised egg contribute equally to embryo development.

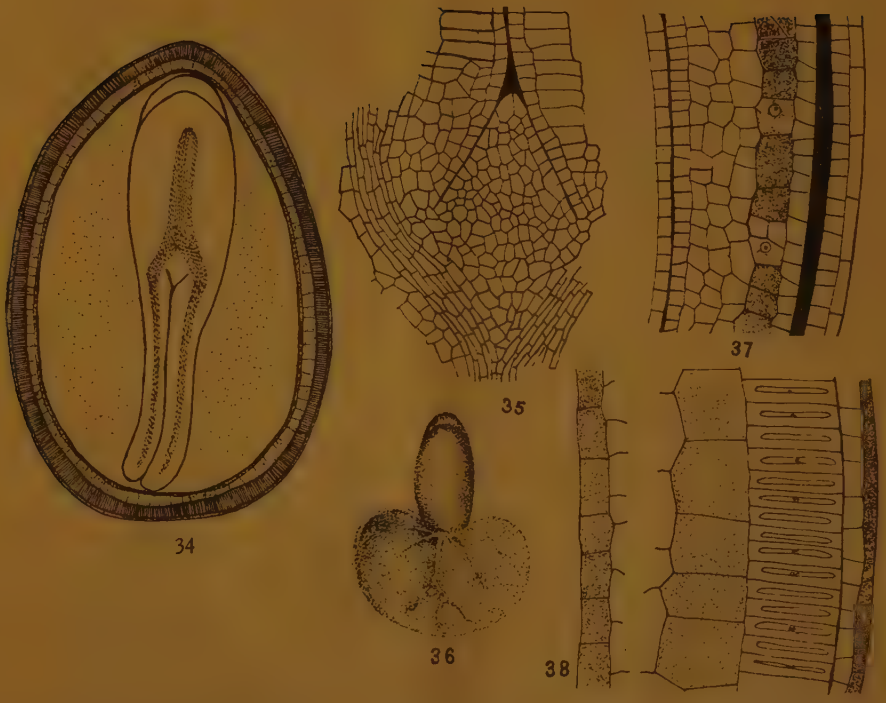
Coincident with the formation of quadrants and octants in the apical tier the two lower cells undergo longitudinal divisions to give rise to quadrants, the divisions in the third cell from the apex being slower than those in the subapical cell (Figs. 27 and 28). Before the third cell from apex undergoes the first longitudinal division, the suspensor cell undergoes a transverse division cutting off an upper cell which functions as the hypophysis-mother cell (Fig. 28). By the time the third cell undergoes the first longitudinal division, the hypophysis-mother cell undergoes a transverse division, cutting off the outer hypophysis cell and an inner cell (Fig. 28). The inner cell, later on, undergoes a transverse division and forms two cells which add to the suspensor (Figs. 29 and 30). Thus the suspensor in *Waltheria* is uniseriate and three cells long. The basal cell, after cutting off the hypophysis-mother cell, enlarges a good deal and develops a characteristic vacuolation which persists for a long time. Its nucleus is always seen to stand near the distal wall.

Periclinal divisions occur when the terminal tier is in the octant stage and proceed in basipetal sequence, demarcating the dermatogen layer to the outside (Figs. 28 and 29). Further divisions in this layer occur in an anticlinal manner so that it remains one cell thick. The inner derivatives of the quadrants divide once again periclinally. The periblem and plerome are thus differentiated (Fig. 30). Further divisions in these initials occur in all planes so that the periblem and plerome become several cells thick in due course. The cotyledon primordia arise as two hump-like outgrowths from the terminal region, while the median region develops into the stem tip, which gets very well differentiated in the mature embryo (Fig. 35). In the full grown embryo, the cotyledons are well developed and foliaceous (Fig. 36). The plerome strands of the cotyledons meet the plerome of the axis just below the stem tip (Fig. 34). The mature seed is endospermic, but without perisperm ; the embryo is straight and measures about 2.5 mm. in length.

The hypophysis cell undergoes the first division, which is longitudinal, after the dermatogen has been differentiated in all the tiers above it (Fig. 31). The next division in the resulting cells is periclinal (Fig. 32).



Figs. 22-33. *Waltheria indica* L. Various stages in the development of the embryo. For further explanation see text. × 500.



Figs. 34-38. *Waltheria indica* L. Fig. 34, L.s. seed. Fig. 35, L.s. through embryo showing stem tip. Fig. 36, entire embryo. Fig. 37, integuments from fertilisable ovule. Fig. 38, structure of seed coats. Fig. 34, × 30 ; Fig. 35, × 170 ; Fig. 36, × 12 ; Figs. 37, and 38, × 300.

By further divisions which occur in all planes in the outer layer, the dermatogen of the root tip and the root cap are formed.

Thus the development of the embryo in *Waltheria* agrees with that of *Melochia corchorifolia* except for the organisation of the suspensor. In *Melochia*, the suspensor remains one-celled for a longer time in the development of the embryo, though ultimately it also becomes three-celled, and the cell cut off by the lowest cell functions directly as the hypophysis cell. In *Waltheria* the cell cut off by the lowest cell functions as the hypophysis-mother cell and after forming the hypophysis cell, gives rise to two cells by a transverse division.

Seed Coats

The outer integument persists as a two cells thick membraneous covering for the seed. The inner integument becomes 10-12 cells thick after fertilisation. The cells of its outermost layer become radially elongate and thick walled, forming the 'palisade' layer which contributes

to the mechanical strength of the seed coat. The walls of these cells are made of cellulose; that they are not lignified is evident by their not staining deeply with safranin. Their lumens also show nuclei and remnants of cytoplasmic contents. The cells below this layer are large and cubical and are filled with deep staining contents. The cells of the innermost layer are tangentially flattened; these cells also accumulate dark-staining contents and in the mature seed get filled with raphides. The remaining 7-8 layers of cells are composed of large thin walled parenchymatous cells, which ultimately get crushed and absorbed (Fig. 38). Thus the structure of the seed coats is closely similar to that of *Melochia* and in general to what has been described in Malvaceæ and Tiliaceæ (Eames, 1947).

Discussion

Waltheria is a genus with about 30 species (Willis, 1948) and is placed by Bentham and Hooker (1862-93) in Sterculiaceæ. Engler and Prantl (1928), on the other hand, place it along with a few other genera of Malvaceæ (of Bentham and Hooker) in a separate family, Bombacaceæ. Hutchinson (1926) while agreeing with Engler and Prantl in the separation of Bombacaceæ, still retains *Waltheria* in Sterculiaceæ. Thus the genus occupies an ambiguous taxonomic position.

Structurally, the flowers of *Waltheria* differ from those of Sterculiaceæ as well as Bombacaceæ in possessing a unilocular pistil with an excentric style. The androecium, however, consisting of five antipetalous stamens with dithecous anthers, resembles that of *Melochia* and differs from that of Bombacaceæ, in which the anthers are unilocular. As the morphological evidence is not decisive, we have to see if its "embryological diagram" clarifies its taxonomic position.

Literature on the embryology of Bombacaceæ is very meagre; as Schnarf (1931) remarks, practically nothing is known justifying the inclusion of the family in Columniferæ. The only genera investigated since then are *Eriodendron* (Thirumalachar and Khan, 1941), and *Bombax* (Banerji, 1942). Even in these the accounts are incomplete in several respects*. Practically nothing is known regarding microsporogenesis and embryogeny. So we must be content for the present with a comparison of the rest of the embryological characters.

Regarding microsporogenesis, a number of features are common to the two families, *e.g.*, the origin of the tapetum from the innermost layer of the wall cells, presence of fibrous endothecium and smooth walled pollen grains. The plasmodial type of tapetum seen in *Waltheria* is found in both Malvaceæ as well as Sterculiaceæ. This feature, however, cannot be regarded as of much taxonomic value since in the single family Sterculiaceæ, some genera like *Guazuma* and *Melochia* show plasmodial type and others like *Dombeya* and *Pterospermum* show secretory type of tapetum. The pollen grains in *Waltheria* are peculiar in showing four germ pores. They thus differ from all investigated genera of Sterculiaceæ (Rao, 1950), as well as *Bombax*, in which they are tricolpate.

* Some of the points given in the subsequent account represent writer's own observations on *Bombax malabaricum*.

A number of characters regarding the structure and development of the ovules and embryo sac are common to the two families and are hence of no taxonomic value. The ovules are anatropous and bitegmic, with a thin outer and a more massive inner integument. Both the integuments take part in the formation of the micropyle which is zig-zag. The ovules show a prolonged period of growth in the megaspore mother cell stage. The nucellus is massive and the parietal tissue is several cells thick. The nucellar epidermis in the region of the micropyle forms an epidermal cap of variable number of cell layers. The ovules show a group of tannin-bearing cells in the chalaza which stain deeply. The archesporium is multicellular to start with and the development of the embryo sac is according to the normal type.

In a number of genera of Sterculiaceæ, like *Dombeya*, *Pterospermum*, *Klienhovia*, *Melochia*, etc., the antipodal end of the embryo sac remains tubular due to the presence of a socket of thick walled nucellus cells around it. But in *Waltheria*, the zone of thick walled cells is seen to subtend and not invest the antipodal end of the embryo sac so that the latter becomes cylindrical, resembling in general form the embryo sacs of *Bombax* and *Eriodendron*. Though uncommon, such a type of embryo sac is not unknown in Sterculiaceæ. In *Sterculia alata* and *S. colorata* studied by the writer, the embryo sac is cylindrical or spherical and has a zone of thick walled cells immediately below it.

Apart from these, there are some embryological features in *Waltheria* which show decisive resemblance to those of Sterculiaceæ. The general appearance of the ovule with its blunt hump-like outgrowth at the chalazal end recalls that of *Dombeya* and *Melochia*. The cytoplasm of the embryo sac in *Waltheria* shows a number of starch grains in which respect it agrees with all the genera of Sterculiaceæ investigated and differs from *Bombax* and *Eriodendron* and also Malvaceæ in general (Schnarf, 1931). The synergids in both the genera of Bombacaceæ are described as pear-shaped and showing a single large basal vacuole ; they do not show lateral hooks. In *Waltheria*, on the other hand, the synergids show two terminal vacuoles and prominent hooks as in other genera of Sterculiaceæ. The polar nuclei in *Bombax* fuse together so that the mature embryo sac is 7-nucleate. In *Eriodendron*, the fusion is reported to occur very early "even before the egg apparatus is organised". In *Waltheria*, however, the polar nuclei do not fuse before fertilisation ; one male nucleus was commonly observed to fuse with one polar nucleus and later a triple fusion nucleus is formed. In this respect, it shows a remarkable resemblance to *Melochia* and *Pterospermum*. The antipodals in *Bombax* and *Eriodendron* are reported to be transitory and are never seen in fully formed embryo sacs. In *Waltheria* they are seen to persist, though in a degenerate condition, till the pollen tube has penetrated the embryo sac. In this respect also it resembles *Melochia*.

Much significance cannot be attached to the evidence of endosperm formation and embryogeny since in all the genera of Malvales investigated so far, there seems to be a remarkable uniformity in these respects. Endosperm formation is free nuclear to start with and becomes cellular later on. The embryo development corresponds, with slight differences, to the *Asterad*-type : *Malva neglecta* (Sougès, 1922, quoted by Schnarf),

Melochia corchorifolia (Rao, 1949*b*), and *Corchorus olitorius* (Banerji, 1932).

From the above account it is clear that the bulk of morphological and embryological evidence points in favour of Hutchinson's view of retaining *Waltheria* in Sterculiaceæ, even when Bombacaceæ is constituted as a separate family.

Summary

The paper deals with the development of the ovule, embryo sac and embryo in *Waltheria indica* L.

1. The ovule is anatropous and bitegmic and shows a zig-zag micropyle formed by both the integuments and a blunt hump-like outgrowth from the chalaza. All the 3-4 layers of cells formed by the primary parietal cell get crushed by the enlarging embryo sac and only the epidermal cap of 2-3 cell layers persists above the mature embryo sac. A *hypostase*-like strand of thick walled cells is seen below the embryo sac.

2. The primary archesporium is multicellular to start with but as a rule, only one cell functions. A linear tetrad of megaspores is formed, of which the lowest megaspore usually functions and forms the 8-nucleate embryo sac according to the *normal*-type. The antipodals persist till the time of fertilisation ; the polar nuclei do not fuse before fertilisation.

3. Fertilisation is porogamous. The pollen tube penetrates first one synergid which later bursts and liberates the male nuclei. One male nucleus fuses first with one polar nucleus and only afterwards a triple fusion nucleus is formed. Endosperm develops according to the nuclear type.

4. The development of the embryo corresponds to the *Polygonum*-variation of the *Asterad*-type. The first division of the fertilised egg is transverse. The terminal cell divides longitudinally and the basal cell transversely. By a transverse division of the lowest cell, the proembryo becomes four cells in length ; of these, the three terminal cells form the embryo and the basal cell forms the suspensor. The terminal cell forms the stem tip and cotyledons ; the subapical cell gives rise to the hypocotyl and the third cell from apex develops into the root tip except its dermatogen and root cap, which are filled out by the hypophysis cell formed form the lowest cell. The suspensor is uniseriate and three cells long.

5. The two cells thick outer integument forms a membraneous cover for the seed. The outermost layer of the inner integument develops into the palisade layer and the innermost layer shows raphides. The remaining 7-8 layers of fleshy cells get crushed.

6. Embryological evidence supports the retention of the genus *Waltheria* in Sterculiaceæ as indicated by Hutchinson and is against its transfer to Bombacaceæ as suggested by Engler and Prantl.

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